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MARTEN ECOLOGY AND HABITAT MANAGEMENT IN THE
CENTRAL ROCKY MOUNTAINS

Lisa A. Bennett

Marten Ecology and Habitat Management in the Central Rocky Mountains



PROBLEM ANALYSIS

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Marten Ecology and Habitat Management
in the Central Rocky Mountains

Problem Analysis

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TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
PROBLEM COMPONENTS AND RESEARCH PROGRAM	5
PROBLEM DEFINITION	13
LIMITING FACTORS	17
PROBLEM BREAKDOWN	19
Network Analysis and Decision Theory Model Applied to Marten and Marten Habitat Management	19
Quantitative Life History	29
1. Demographic Parameters	29
2. Seasonal Marten Movements and Habitat Use	32
Seasonal Diet, Prey Distribution, Foraging Energetics	36
1. Seasonal Diet	36
2. Prey Distribution	38
3. Foraging Energetics	40
SUMMARY	48
LITERATURE CITED	50

INTRODUCTION

Historically, the marten (Martes americana) (Jones et al. 1982) was distributed throughout the northern coniferous forests of North America (Hagmeier 1956). This forest is predominantly composed of pines (Pinus spp.), spruce (Picea spp.), and fir (Abies spp.). The forest extends east-west from the Atlantic to the Pacific Ocean, south to include the northern Appalachian and Rocky Mountain ranges, through the upper Great Lake states of Minnesota, Wisconsin, Michigan, Illinois, and Ohio, and north to the edge of the tundra in northern Canada and Alaska.

The current range of the marten is a small portion of the historic range. Marten have been extirpated in Illinois, Michigan, New Hampshire, Ohio, Pennsylvania, Vermont, West Virginia, and Wisconsin (Deblaay 1980). Moreover, extensive range reductions and substantial declines in the size of local populations have been reported in Newfoundland (Bergerud 1969), Nova Scotia (Dodds and Martell 1971), California (Schempf and White 1977), and Minnesota (Mech and Rogers 1977). As early as 1909, Seton (1909:906) noted, "The species is indeed becoming scarcer every year in all the southern parts of its range"

The decline in marten population size and range is attributed to extensive habitat destruction, primarily through unregulated deforestation (Yeager 1950, Marshall 1951, Remington 1951, Miller et al. 1955, Harger and Switzenberg 1958, Maxham 1970, Dodds and Martell 1971, Brown 1980) and fire (Brabant 1922, Lutz 1956, Maxham 1970, Brown 1980). Overtrapping (Grinnell et al. 1937, Yeager 1950, Marshall 1951, Remington 1951, Harger and Switzenberg 1958, Dodds and Martell 1971, Haley 1975, Brown 1980) and predator control (Marshall 1951) are two

additional factors detrimental to marten populations. Seton (1953:497) observed, "Man is, of course, the chief enemy of the marten, . . . I do not know one case in which a man came in contact with a marten without trying to kill it." Unfortunately, the situation is not unique to M. americana as habitat destruction and fragmentation, along with predator control, has extensively reduced the range and population numbers of the closely related European species, M. martes (Langley and Yalden 1977, O'Sullivan 1983).

Three major factors make the marten vulnerable to local extirpation and extinction. First, like most carnivores, martens have a low biotic potential. Females mate at two years of age and, due to delayed implantation (Ashbrook and Hanson 1930, Marshall and Enders 1942), young are not produced until age three (Marshall 1951, Ingles 1965, Soutiere 1978). Estimates of litter size range from one to six (Grinnell et al. 1937, Ingles 1965, Maser et al. 1981), with 2.6 to 4 reported as average values (Seton 1909, Marshall 1951, Deblaay 1980). Although no estimates of juvenile survivorship are available, observations by Grinnell et al. (1937:200) led them to suggest, ". . . the number of young which reach maturity each year is remarkably small." In addition, the average number of litters produced by a female is not known, nor are longevity data available.

Second, martens exhibit an affinity for overhead cover and avoid extensive use of open areas, especially in winter (Hawley and Newby 1957, Koehler and Hornocker 1977, Simon 1980, Spencer 1981, Wynne 1981, Zielinski 1981). Significantly, females are less apt to cross open areas than are males (Soutiere 1978, Steventon 1979, Steventon and Major

1982). Use of areas with overhead cover has also been documented for M. martes in northern Europe (Pulliainen 1981).

Marten have traditionally been considered a climax or near-climax species (Miller et al. 1955), intolerant of human presence (Seton 1953, Ingles 1965). Ingles (1965:369) stated, ". . . human ways and marten ways do not seem to be at all compatible." However, tolerance and adaptability of martens have also been observed (Hawley 1955). In fact, Spencer (1981) noted an attraction of marten to man-made structures. New, multiple-use forest management may prove compatible with marten population maintenance (Miller et al. 1955, Koehler et al. 1975, Soutiere 1979). Selective harvesting, small clear-cuts interspersed within a mature forest, and maintenance of dead-wood components within the forest stand may help retain marten life requisites. In fact, Koehler et al. (1975:33) stated, "Although large, homogeneous mature forest may support more marten over a given area, a diversity of forest communities may support more marten over time." Recently, several studies have assessed marten habitat requirements (Soutiere 1978, Campbell 1979, Simon 1980, Spencer 1981); however, the data are frequently locally applicable and, for the most part, incomplete.

The marten's large home range is a third factor making them vulnerable to extirpation. Home range estimates based on relocations of radio-collared animals range from 5 to 15.7 km² (1.9 to 6.1 mi²) for males and 2 to 4.3 km² (0.8 to 1.7 mi²) for females (Mech and Rogers 1977, Wynne 1981, Steventon and Major 1982). This large home range, combined with their reported curiosity (Seton 1909) make marten vulnerable to trapping (Grinnell et al. 1937, Hawley 1955, Miller et al. 1955, Dodds and Martell 1971). Natural colonization of "trapped out"

areas is slow because of the large home range, sedentary nature of female marten (Lensink 1954), and low reproductive capacity. Moreover, to date most reintroduction attempts have failed (Haley 1975, Deblaay 1980). Successful marten reintroductions may have been accomplished in southern Ontario (Strickland et al. 1982), Wisconsin, and Michigan (H. Donoho, pers. commun.). However, maintenance of existing populations appears to be the most feasible management strategy for continued existence of martens.

This problem analysis focuses on marten ecology and habitat management for four major reasons: (1) decreases in range size and local extirpations have caused concern for species maintenance; (2) low biotic potential, large home-range size, and curious nature, combined with habitat loss and fragmentation, make the marten vulnerable to localized extinction; (3) the size and distribution of forest vegetation age classes required to maintain marten populations are unknown; and (4) the marten is potentially a good indicator species, serving as a "barometer" of ecosystem health (Koehler et al. 1975).

PROBLEM COMPONENTS AND RESEARCH PROGRAM

The problem--that knowledge of factors governing marten distribution and abundance is inadequate for quantitative prediction and evaluation of the effects of forest management practices on marten populations--is divided into three components. The first component is a regional population-planning model. Decision theory and network flow analysis may be integrated to provide a useful, quantitative approach for predicting the probability of maintaining different population levels. This would include assessing the risks of regional population extinction under alternative forest management strategies. The second component examines marten life history. Quantitative information is required to describe marten reproductive biology, population dynamics, movements, and habitat use. The third component addresses marten niche relationships. Data are needed to establish the effect of prey availability, marten diet, and foraging energetics on seasonal marten movements, habitat use, and demographics.

Seven integrated studies are proposed to provide the needed information. Each study will address questions concerning marten ecology and life history and will be conducted in an experimental framework. The studies should be replicated in at least two forest vegetation age classes--one primarily old-growth forest; the second in an area with one or more vegetation age classes representing the age classes within the successional stages leading to a climax, or old-growth, forest. The forest vegetation age classes are needed in a variety of sizes and dispersion patterns to refine the decision theory model.

Component I: Network Analysis and Decision Theory Model
Applied to Marten and Marten Habitat Management

Forest and wildlife managers are faced with the challenge of maintaining viable populations of marten--that is, minimizing the risks of local marten extirpation due to other forest uses. There are no studies or methods reported in the literature to date that allow a manager to make a quantitative assessment of the risks of local population extinction associated with different forest management strategies. Network flow analysis and decision theory provide a means of simulating local and regional marten population dynamics in a mosaic of habitat patches that vary in size, shape, and location over time.

A network is an assemblage of nodes, connected by arcs (Jensen and Barnes 1980). Each node in the network may be viewed as a local marten population (or patch of marten habitat) and as part of a regional or metapopulation. The dynamics of each nodal (local) population and the immigration, emigration, and within-node dynamics can be analyzed using decision theory. Decision theory provides a framework within which benefits and costs of alternative strategies may be probabilistically analyzed to produce an optimum solution. For example, a marten within a nodal population makes "decisions" to emigrate or stay in a nodal patch and to breed or not to breed, based on the relative costs (e.g., survival) of each decision relative to potential benefits (e.g., survival and successful reproduction). The size, quality (e.g., carrying capacity), and distribution of nodes depends on the mosaic of different vegetation cover types and structural classes within a national forest (or within a regional administrative network). By integrating decision theory and network analysis concepts with the inventory of forest

habitat conditions, a model can be developed that will allow a forest manager to evaluate a series of management alternatives in terms of the probabilities of marten extinction associated with each alternative. Thus, an optimum choice of forest management strategies can be obtained, allowing for a high likelihood of continued existence for the marten population, along with other multiple uses.

I.1 Title: Network flow analysis and decision theory: An integrated, quantitative model to plan forest management for marten population goals.

Objectives:

- A. Develop a model, based on existing technology and information, that allows quantitative prediction of the likelihood of localized marten population extinction associated with alternative forest management strategies.
- B. Test selected assumptions and predictions of the model with data obtained from extensive and intensive field study conducted under components II and III.

Component II: Quantitative Life History

Better information on marten life history is needed to effectively manage and maintain marten habitats and populations in the central Rocky Mountains. Knowledge of the intrinsic rate of increase ($\underline{r}$) for martens is required to predict future local population size and to determine the viability of an existing local population. This parameter is defined by the relation $\underline{r} = \ln \underline{R}_0 / \underline{T}$, where $\ln \underline{R}_0$ is the natural logarithm of the net rate of reproduction per generation and $\underline{T}$ is generation time (Krebs 1972). Both $\underline{R}_0$ and $\underline{T}$ vary with environmental conditions. When $\underline{R}_0$ is maximum for the species and $\underline{T}$ is minimum, $\underline{r}$ becomes the maximum possible intrinsic rate of population growth ($\underline{r}_m$) for the species. Among mammals, generation time increases with gestation period and with the

time after birth required to reach reproductive age. $\underline{R}_0$ is a function of litter size and the number of litters a female will have in her lifetime, which, in turn, are related to age-specific fecundity and survivorship schedules (Ricklefs 1979). In addition to $\underline{R}_0$ and $\underline{T}$, reproductive capacities of specific local populations will be influenced by immigration and emigration.

The U.S. Forest Service is required by the National Forest Management Act of 1976 to manage habitats to maintain viable populations of naturally occurring vertebrate species throughout their geographic ranges. The U.S. Fish and Wildlife Service, under the guidance of the Fish and Wildlife Coordination Act of 1958 (as originally passed in 1934 and amended in 1946, 1948, and 1958, P.L. 85-624), has developed a Habitat Evaluation Program to mitigate and compensate for the effects of habitat loss. In addition, the State of Colorado is expected to manage all wildlife species to maintain populations. To meet these legal obligations, Federal and state agencies gather and apply quantitative information to build models of wildlife habitat relationships.

The marten Habitat Suitability Index (HSI) model (Allen 1982) was developed to evaluate the quality of winter habitat for marten. Model parameters are restricted to those quantitatively related to key environmental variables and habitat suitability for marten. This HSI model assumes that adequate food resources will be available if adequate cover is provided, and thus calculates habitat suitability based solely on the life requisite for winter cover. The life requisite for winter cover is composed of percent tree canopy closure, percent of overstory canopy closure composed of fir or spruce, successional stage of stand, and percent of ground surface covered by downfall. Synthesis of these

habitat variables yields an index value between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). The model was developed for use in boreal coniferous forests of the western United States. T. Clark (pers. commun., Idaho State Univ. in Allen 1982) stated that this HSI model would provide an accurate evaluation of habitat suitability for marten.

Barrett and Spencer (1982) developed a habitat suitability index and evaluated the effectiveness of this model in the Sierra Nevada, California. Food, cover, and den sites were included as life requisites. There was a significant ($P < 0.05$) but weak ($r^2 = 0.59$) correlation between habitat suitability predicted with the model and marten habitat use. They revised the model to increase the importance of cover and detail requirements for adequate interspersions, and obtained an improved fit of the model ($r^2 = 0.75$). However, this model remains untested for use in the central Rocky Mountains.

We propose two studies that will allow comparisons regarding the capabilities of the HSI model, as developed and modified by Barrett and Spencer (1982), to predict habitat suitability for marten. These studies will compare predicted marten habitat suitability with quantitative analyses of actual marten habitat use and demographic patterns observed in the field.

Specific objectives in regard to the quantification of marten movements and habitat use will be to examine marten distribution and abundance patterns relative to the availability of preferred habitat. Habitat variables examined should be factors controlled by forest management and should include cover-type variables such as vegetative diversity, Society of American Foresters types, and plant associations. In addition, structural variables such as basal area, dbh, crown

closure, midstory and understory characteristics, and densities of snags, fallen trees, litter, and slash, should be considered. Finally, the spatial patterns of different stands should be included to assess regional population effects.

II.1. Title: Demographic parameters of marten populations in the central Rocky Mountains.

Objectives:

- A. Determine generation time and litter size.
- B. Determine the percentage of females producing young per year and the number of litters produced by a female.
- C. Determine age- and sex-specific survivorship schedules.
- D. Determine immigration and emigration patterns.

II.2. Title: Seasonal movements and habitat use by marten.

Objectives:

- A. Assess seasonal use of forest vegetation age classes by marten and determine habitat characteristics unique to areas intensively used by marten.
- B. Document daily, seasonal, and annual movements within and between habitat patches that vary in age, size, and distance from similar habitat patches.

II.3. Title: The marten HSI model: A quantitative evaluation.

Objectives:

- A. Compare the habitat suitability index based on local habitat conditions with relative use (frequency of occurrence or relative abundance) by marten in the area.
- B. Determine the reliability of inferring marten population parameters from HSI models, using one, two, three, or more habitat variables beginning with the easiest and least costly to measure.

Component III: Seasonal Diet, Prey Distribution, Foraging Energetics

There have been few inquiries into the significance of variation in energy flow in population ecology. This involves an evaluation of the rate of energy acquisition and rate of energy expenditure. Foremost among the factors in energy acquisition are foraging effectiveness, food habits, and prey availability. Major energy expenditures are influenced by the environmental extremes, the rate of metabolism, growth rate, fecundity, and gestation period. These factors also directly affect the intrinsic rate of a population's growth (r), which is needed to determine population viability.

To assess the importance of energy availability in regulation of marten populations, three integrated studies are suggested. Specifically, these studies should assess (1) the volume and rate of energy flow through an individual marten, along with consideration of the seasonal variability in this flow; (2) the relationship between prey availability and fluctuations in marten demographics; (3) the effect of age and sex structure of marten populations on energy requirements; and (4) the relationship between seasonal energy flow in a marten population and the availability of prey items needed to satisfy that flow.

To understand foraging energetics of marten, knowledge of the factors that influence the distribution and abundance of small mammals, the principal prey of marten, is needed. Numerous authors have noted that foliage height diversity, vegetation density, and soil structure explain variation in rodent species distributions both within and between habitats. Quantitative assessment of small mammal microhabitat preferences should include variables that measure environmental structure known or suspected to be important to small mammal distribution and

abundance. One should be able to measure the environmental variable(s) quickly with accuracy and precision, using nondestructive-sampling procedures and expect to have small intraseason variability compared with interseason variability (Green 1971, Dueser and Shugart 1978, Noon 1981).

- III.1. Title: Occurrence and diversity of prey species in the marten diet, with emphasis on winter diet.

Objective: Determine seasonal marten diet with emphasis on small mammals in the winter diet.

- III.2. Title: Abundance, distribution, and habitat use of prey species in the marten diet.

Objectives:

- A. Determine the distribution and abundance of small mammals within the range of forest vegetation age classes used by marten.
- B. Compare microhabitats used by small mammals and examine the relationships of small mammal distribution and abundance patterns to microhabitat availability in different forest vegetation age classes.

- III.3. Title: Population dynamics and bioenergetics of the marten.

Objectives:

- A. Determine individual marten energy flow patterns along with seasonal variations in these flows.
- B. Determine the relationship between small mammal prey availability and marten demographics.
- C. Determine the effect of age and sex structure on energy requirements of marten populations.
- D. Determine the relationship between seasonal energy flow required by marten populations and availability of prey items to satisfy that flow.

PROBLEM DEFINITION

Extensive deforestation, fires, unregulated trapping, and predator-control programs have contributed to the decreased marten population and fragmented marten range. As historically conducted, logging and trapping appeared incompatible with marten population maintenance. However, recent research (Koehler et al. 1975, Soutiere 1978, Major 1979) has cited potential compatibility between contemporary human and marten activities. The analytical challenge is to identify and relate marten life requisites to habitat parameters under the control of foresters and wildlife biologists. In addition, this must be done in a way that will explain marten population presence and abundance.

Marten have been described as a climax or near climax forest species (Miller et al. 1955). However, several forest types are used by marten, with some variation by season and sex. In Idaho (Marshall 1951, Koehler et al. 1975), Ontario (de Vos et al. 1959, Taylor and Abrey 1982), and Wyoming (Campbell 1979), marten are most active in mature coniferous forest. In Colorado, marten are typically most abundant in dense lodgepole pine (Pinus contorta) or spruce-fir (Armstrong 1972). Burgason (1977) reported that marten preferred softwoods in Maine but also used other aged forest stands in proportion to availability. Maser et al. (1981) noted that marten along the Oregon coast are usually found in dense, mature conifer swamps but will travel through other vegetation types. Brown (1980), working in New York, located marten in hardwood, mixed wood, and softwood stands, including hardwood stands with active timber harvest in progress. In Ontario, during summer, Standfield (1956) found marten in coniferous forest bordering streams and lakes, mixed soft and hardwood stands near water, and on high hardwood ridges.

Koehler and Hornocker (1977), in Idaho, as well as Spencer (1981), in California, found marten in a variety of forest types; but each type had similar structural characteristics. In both studies, it appeared that marten avoided areas with less than 30% overhead cover. In general, Spencer (1981) determined that marten preferred relatively dense forest, close to meadows, with many large stumps, fallen trees, and snags. Thus, it appears that marten use a variety of forest stands as long as they contain key structural elements related to food and cover.

Marten make little use of extensive open areas, especially in winter (Seton 1953, Hawley and Newby 1957, Herman and Fuller 1974, Simon 1980, Spencer 1981, Steventon and Major 1982). Seton (1953:487) noted, ". . . the merest beginning of a clearcut about the settler's home is enough to drive it away." Estimates of the size of openings marten will cross vary considerably. Simon (1980) found that the largest opening marten would cross during all seasons was 40 m. Marten studied by Koehler and Hornocker (1977) would cross 100 m-wide openings in winter but would not hunt in these areas. Spencer (1981) reported that marten rarely ventured more than 10 m into openings and suggested that this was because of predator avoidance. Herman and Fuller (1974) also suggested that this aversion to open areas is a means of predator avoidance (this was based on observations of one female with an old, healed wound that was especially sensitive to a raven shadow). Newby (1951) also observed that marten used meadow edges rather than openings in the forest. However, he felt that this was because of hunting habits, not predator avoidance. Hawley (1955) and Simon (1980) suggested two hypotheses for travel along the meadow edge: (1) prey availability may be greater

along meadow edges than in a contiguous forest, or (2) marten may be reluctant to leave the forest cover.

Some occasional use of open areas, including rock outcrops and rockslides, has been documented (Grinnell et al. 1937, Streeter and Braun 1968, Lutton 1975, O'Neil 1980). In addition, Jones (1955) found one male marten killed by a car approximately 6.5 km (4 mi) from the nearest tree and roughly 12.9 km (8 mi) from "typical" marten habitat. Murie (1961) observed a marten using rocks as protective cover from a prairie falcon (Falco mexicanus) approximately 0.8 km (0.5 mi) from the nearest timber.

Both the affinity for moderate to dense overhead cover and avoidance of extensive open areas influence marten use of timber management areas. In northern Maine, Burgason (1977) found that uncut softwood was used more and 14 to 16 year-old clear-cuts were used less often than expected, based on availability. Hardwoods, 20 to 25 and 6 to 10 year-old softwood clear-cuts were used in proportion to their availability. Soutiere (1978), who also worked in Maine, observed that marten rarely used 0 to 15 year-old clear-cuts. Clear-cuts had approximately one-third the marten density of partially-cut and uncut timber, marten on clear-cuts had larger home ranges, and fewer immature and transient animals were captured in clear-cut areas. Soutiere (1978) did not find decreased food availability on the clear-cuts, but suggest that accessibility may have decreased. Steventon (1979), working on the same study area as Soutiere (1978), also reported that marten used uncut softwood and partially-cut mixed wood extensively, while clear-cuts were used less than expected. Churchill et al. (1982) documented a male marten hunting and killing a snowshoe hare (Lepus americanus) in a clear-cut.

Females are less likely than males to cross open areas (Soutiere 1978, Steventon 1979, Steventon and Major 1982). Steventon and Major (1982) documented one male that traveled 1.7 km through a clear-cut. The average distance males traveled through clear-cuts was 0.36 km, while females averaged 0.14 km. Steventon (1979) observed that females were captured only in large patches of forest cover, estimating that females would not cross openings greater than 300 m. Soutiere (1978) reported that female marten exhibited less flexibility in habitat use than did males. While males ranged over most of the forest, including clear-cut areas and uncut residual softwood stands, females made little use of clear-cuts and were absent from the smaller softwood islands and islands far from residual cover.

In summary, marten habitat use is variable over time and between sexes. Current knowledge of factors governing marten distribution and abundance is adequate only for qualitative prediction and evaluation of the effects of forest management practices on marten populations. That is, we can predict marten responses to extreme conditions (e.g., all mature forest versus all meadow or clear-cuts). However, we cannot accurately predict marten population responses as we add different sizes and total amounts of openings to a block of mature forest or change dispersion patterns of mature forests on a regional basis.

LIMITING FACTORS

Although correlative and qualitative observations concerning the importance of prey items to marten abound, quantitative data relating food availability to marten requirements are lacking. The available data do suggest that food availability is a proximate factor limiting marten numbers.

The hypothesis that food regulates marten populations is substantiated in a number of ways. Marten usually begin hunting shortly following release from a trap, indicating that hunting is a high-priority activity (Hawley 1955, Lensink et al. 1955, Simon 1980). Individuals live trapped repeatedly over a short period often show a precipitous decline in body weight (Newby and Hawley 1954, Hawley 1955, Weckwerth 1957), with death sometimes the result (Weckwerth 1957). Females and juveniles seem to be most vulnerable to trap mortality, presumably because of their high energy demands for reproduction and growth (Hawley 1955, Hawley and Newby 1957, Weckwerth 1957, Soutiere 1978).

Trap success, population size and condition, and dispersal rates have been correlated with changes in small mammal populations (Hawley 1955, Hawley and Newby 1957, de Vos et al. 1959, Weckwerth and Hawley 1962, More 1978, Soutiere 1978). Soutiere (1978) and Hawley and Newby (1957) correlated a decrease in marten body weight with a decline in small mammal populations. Weckwerth and Hawley (1962) documented decreased production of young marten with small mammal population declines. Decreased marten activity in winter has been suggested to result from food and cold stress (Zielinski 1981). Moreover, home ranges are often larger in winter than during snow-free periods (Miller et al. 1955, Weckwerth and Hawley 1962); the larger size perhaps

indicates food scarcity (Dulkeit 1929, Marshall 1942, Yeager 1950, Lensink et al. 1955). Trap success, usually higher in winter (Newby 1951, Hawley 1955, Miller et al. 1955), is probably inversely related to food availability, since marten appear to range over larger areas when food is scarce. Yeager (1950) and Quick (1953b) found that an increased proportion of female marten was harvested later in the trapping season [although see de Vos et al. (1979) for a contradictory viewpoint], perhaps because of food scarcity in midwinter aggravated by high energy demands on females. Moreover, marten body weights may decline over winter (Newby and Hawley 1954).

A second potentially limiting factor is availability of water. Although this hypothesis remains uninvestigated, several observations are relevant. Marten frequently hunt drainages and wet areas within timber stands (Simon 1980). Hawley (1955) noted that released individuals ordinarily went directly to water in summer or ate snow in winter. Lensink et al. (1955:366) noted similar marten behavior, observing, ". . . an animal which had become thirsty while in the live-trap dug into the moss to obtain water as soon as it was released." Moreover, it has been suggested that the distribution of the marten's primary food item, the red-backed vole (Clethrionomys gapperi), is governed by free water availability (Gunderson 1959). The potential importance of water availability to marten should be examined, along with other habitat parameters.

PROBLEM BREAKDOWN

Network Analysis and Decision Theory Model Applied to Marten and Marten Habitat Management

Currently, forest managers are confronted with the challenge of maintaining viable marten populations, weighing the risks of marten extirpation with the values of other forest uses. Although a percentage of a national forest may be set aside to remain as climax or "old-growth," the shape, size, and distribution of most old-growth habitat patches are frequently a result of the timber management program.

The habitat dispersion problem is especially relevant to the marten. Marten appear to be restricted to patches or island of mature to old-growth forest, and movement between islands is restricted to forested "corridors." For example, Harris et al. (1982) found the median size of old-growth stands in the Siuslaw National Forest, California, to be 12.6 ha (31 ac), with interpatch distances approaching 18 km (5 mi). Accepting the limited knowledge available on marten home ranges and dispersal distances, the likelihood of maintaining a viable marten population on islands so small appears limited; a 13-ha patch may support only one adult. However, whether the patches are connected with travel corridors or are in a matrix of clear-cuts would have an influence on the chances of marten population maintenance. Network analysis and decision theory will provide a means to simulate local and regional marten population dynamics in a mosaic of habitat patches that vary in size and distribution. Therefore, land-management alternatives can be analyzed to determine which will minimize the risk of marten extinction over the area of concern.

A network can be represented as an assemblage of nodes connected by arcs (Jensen and Barnes 1980). As applied to marten, nodes are habitat patches with flows of marten between them. Using the Out-of-Kilter Algorithm (OKA) (Ford and Fulkerson 1962 in Jensen and Barnes 1980), a computerized network flow model is constructed to simulate between-patch flows, yielding an estimate of within-patch population size as well as population size over an entire region. The OKA allows three parameters to be specified on the arcs, including cost per unit flow (c), along with upper (u) and lower (l) bounds on flow volume (Fig. 1). The lower limit on flow in the case of a marten population is zero, as all animals may potentially stay in their natal habitat patch. Conversely, the upper flow limit could be the total number of individuals in the population or the segment of the population most likely to disperse (juveniles and perhaps adult males). The costs per unit flow are a function of habitat suitability and marten density in the patch the animal would be leaving and the probability of survival over the interpatch distance.

Decision theory (Lifson 1972, Anderson 1982) provides a framework within which benefits and costs of alternative strategies are analyzed to produce an optimum solution. A marten in a habitat patch must make a "decision" to emigrate or stay in its natal habitat patch based on the relative costs of remaining in a patch compared with the cost of dispersing in hope of locating suitable habitat elsewhere. This decision process can be represented for the marten using a survival curve based on the probability of individual survival given the marten density currently existing within a patch.

For model development, marten home ranges of 2.9 km^2 for males and 1.1 km^2 for females (Major et al. 1981) or 4 km^2 for one pair with

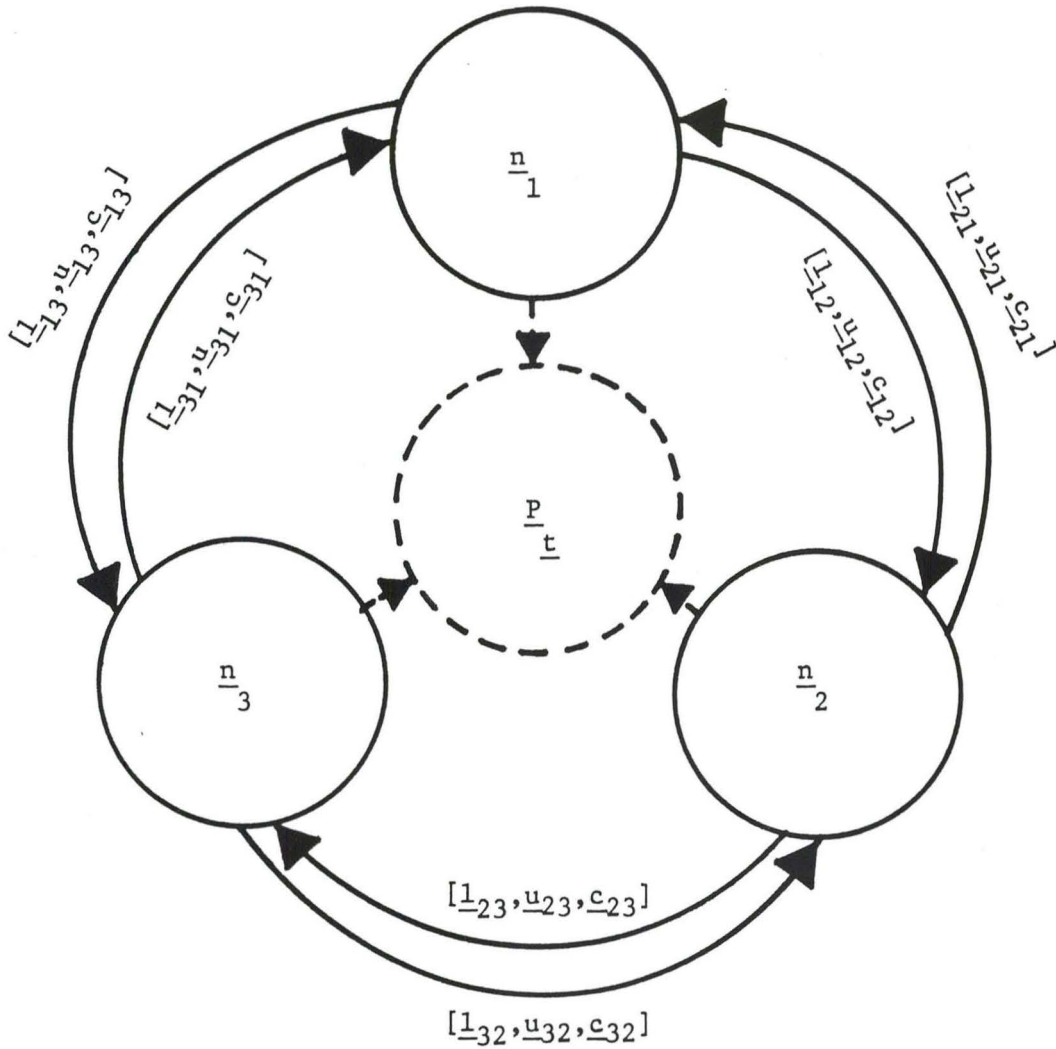
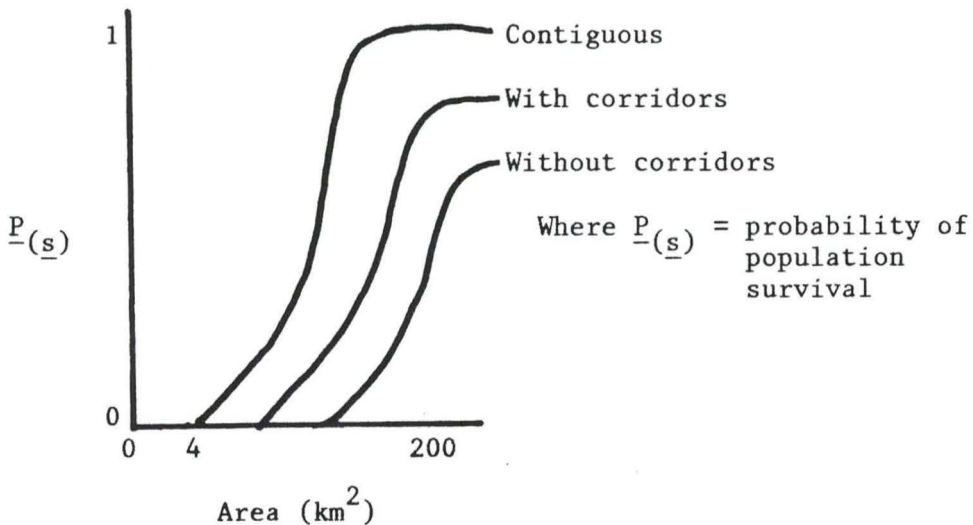


Fig. 1. A graphic representation of a network, defined as a series of nodes ($\underline{n}$) connected by arcs (solid line). Parameters defined along each arc include the cost of travel from one node to another ($\underline{c}$), along with the lower ($\underline{l}$) and upper ($\underline{u}$) bounds on flow volume. These parameter values may be separately defined for each arc, as illustrated by the subscripts. Dotted lines indicate a net value or total population size ($\underline{P}_t$) for the sum of habitat patches over a region or forest.

exclusive home ranges were chosen. Estimates of marten home range size are related to the method and number of relocations. Estimates of home range size obtained with live trapping tend to yield estimates only 8-32% as large as radiotelemetry data (Major et al. 1981). However, the home range used for this model is conservative relative to the range of radiotelemetry estimates reported in the literature (5 to 15.7 km² for males, 2 to 4.3 km² for females) (Mech and Rogers 1977, Wynne 1981, Steventon and Major 1982). If one assumes 50 breeding pairs are needed for local population viability [although 500 breeding individuals with an equal sex ratio has been suggested by Frankel and Soule (1981)], this would yield 200 km² needed for a viable marten population.

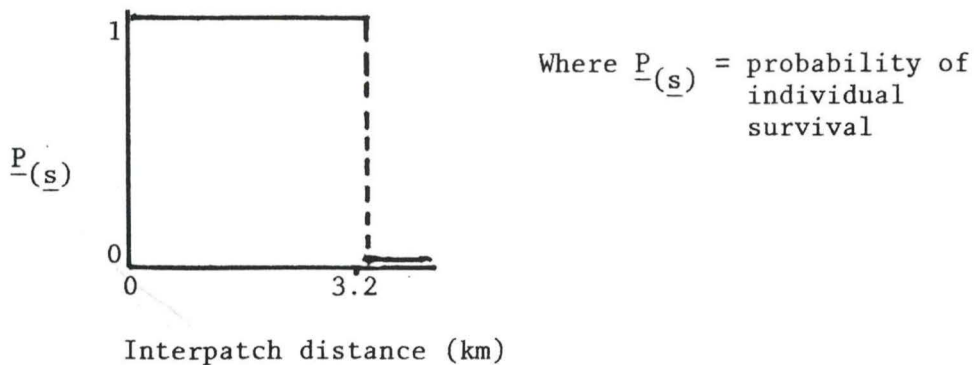
An approximation of the probability of population survival, given different area sizes and management regimes, is shown below.



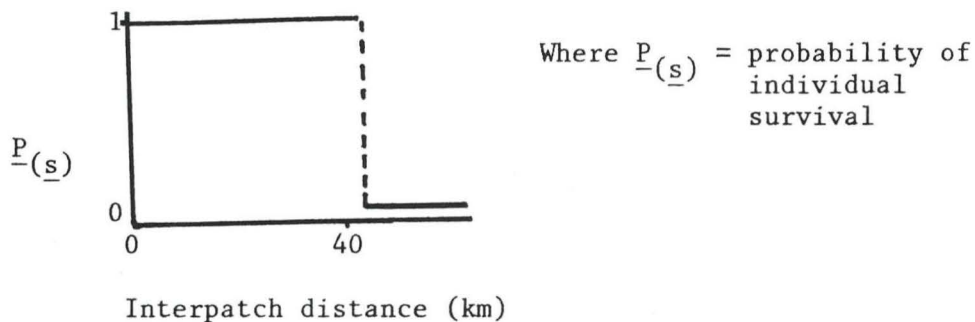
Note that a series of curves relate to dispersion of the patches. Contiguous patches would have the highest probability of maintaining marten populations, while isolated patches without travel corridors would have the least, for a given size of area. To obtain better

estimates of extinction probabilities, it is necessary to simulate interpatch population dynamics. Importantly, Schonewald-Cox (1983) has developed a hierarchy of species protection levels based on interpatch population dynamics, which has been modified by Salwasser (1984) for future use in national forest planning and habitat management.

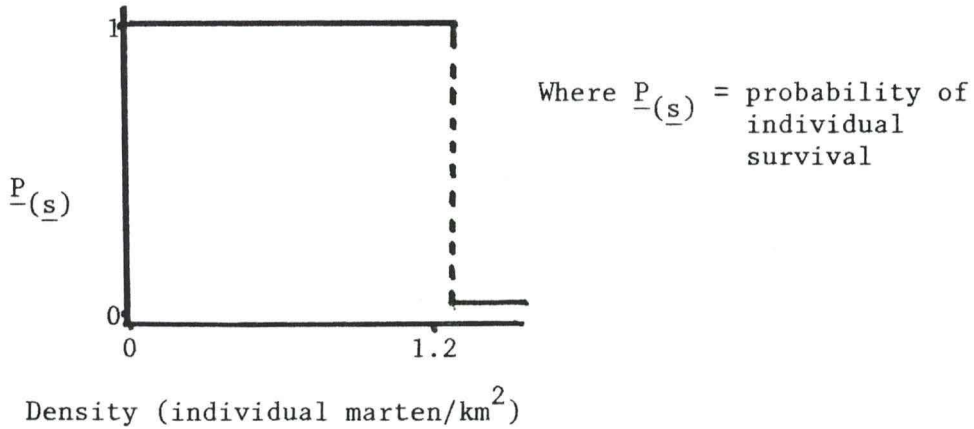
Using several parameters available in the published literature, travel cost functions can be estimated. Streeter and Braun (1968) found marten in boulder fields 0.8-3.2 km from forest, and Hawley (1955) stated that marten will travel up to 40 km to establish themselves in good habitat. For initial modeling purposes, approximations of travel costs without corridors are as follows:



The travel function with corridors is likely to be of similar shape but with a higher probability of marten survival over longer distances.



Burke (1982) termed normal marten densities 0.4-1.2 individuals/km². For this model, it is assumed that at densities greater than 1.2 individuals/km², the cost of staying in a patch is greater than the cost of emigrating. Age three is used as the first year of female reproduction.



A simple, hand-calculated example of the model over two time steps and using two patches is illustrated below. With more than two patches or with more time steps, calculations become enormous and a computer routine is essential. Graphic presentations of time steps one and two are shown in Figs. 2 and 3, respectively.

Year One

Population: Population size is 24, consisting of 12 pairs (12 males and 12 females). Female age structure is: four 1 year-olds, four 2 year-olds, and four 3 year-olds. Therefore, four females are of reproductive age and assumed to produce litters, usually of two to three young each. Population production is shown below:

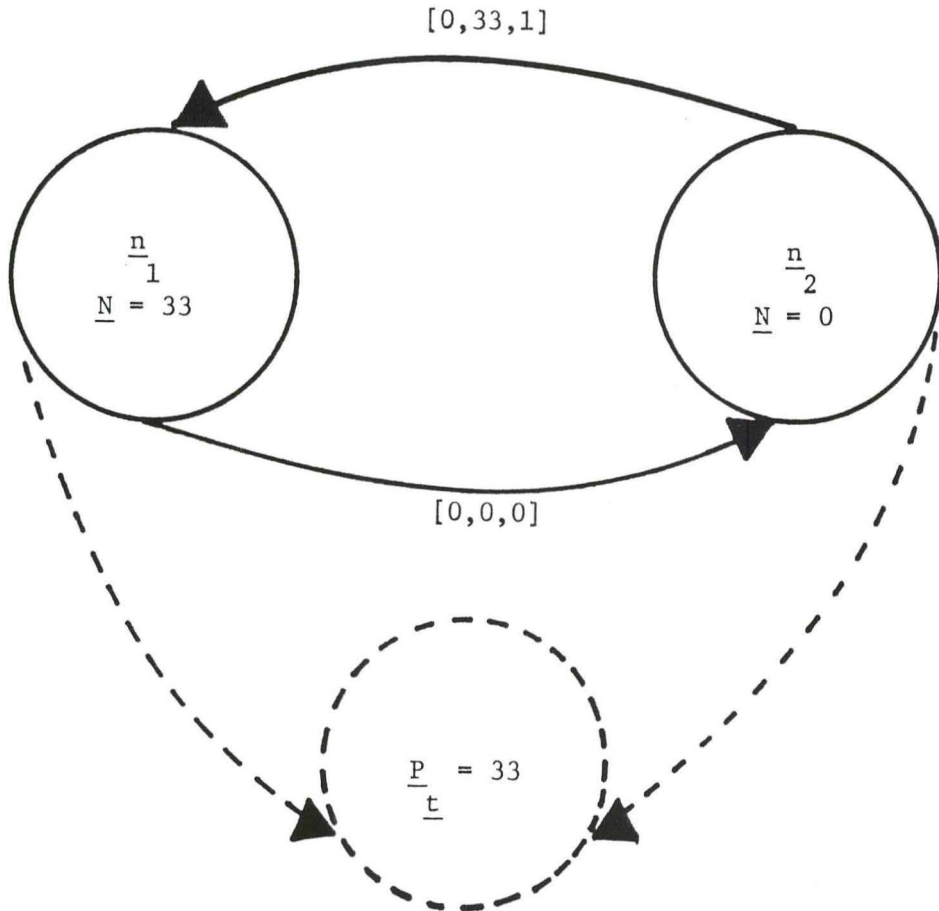


Fig. 2. Network flow model illustrating the population dynamics of a hypothetical marten population in two habitat patches in year 1. Parameters identified on the arcs are lower bounds on flow volume, upper bounds on flow volume, and cost per unit flow, respectively. Flow is arbitrarily defined to occur when cost per unit flow is zero and to be unfeasible when cost per unit flow is one. Size of patch 1 ($\underline{n}_1$) and patch 2 ($\underline{n}_2$) are 35 and 3 km², respectively; $\underline{n}$ indicates within-patch population size. Dotted lines indicate a net value or population size ($\underline{P}_t$) for the sum of habitat patches over a region or forest.

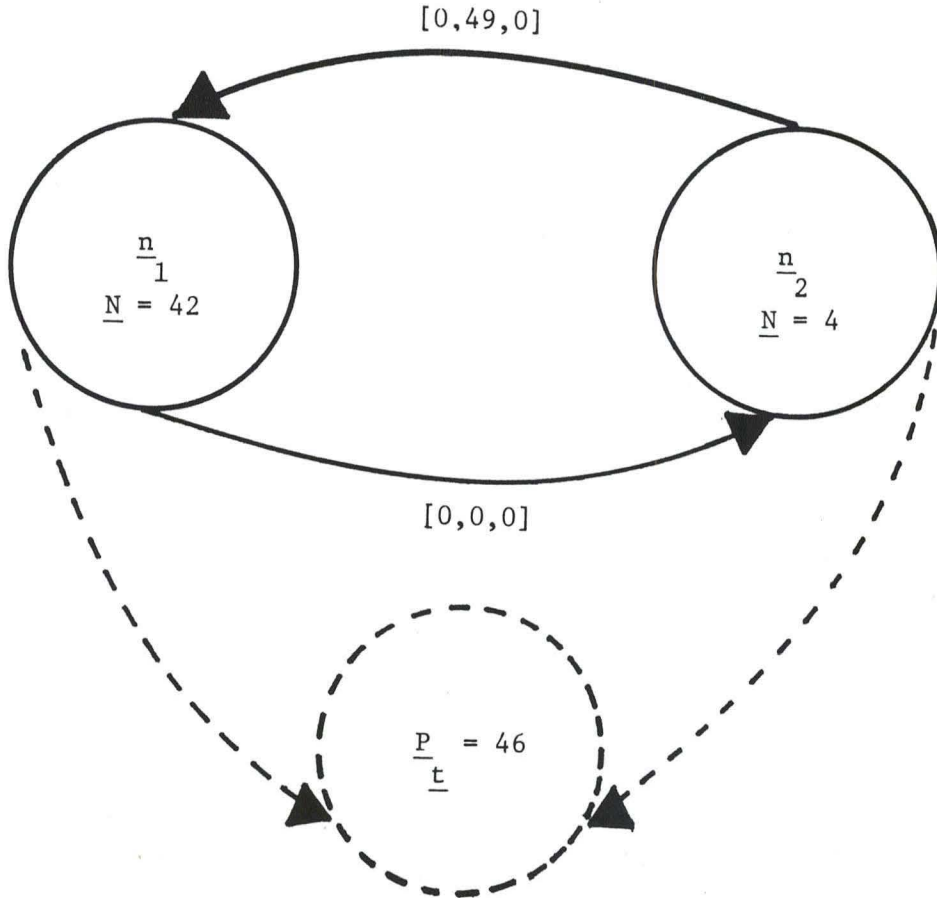


Fig. 3. Network flow model illustrating the population dynamics of a hypothetical marten population in two habitat patches in year 2. Parameters identified on the arcs are lower bounds on flow volume, upper bounds on flow volume, and cost per unit flow, respectively. Flow is arbitrarily defined to occur when cost per unit flow is zero and to be unfeasible when cost per unit flow is one. Size of patch 1 ($\underline{n}_1$) and patch 2 ($\underline{n}_2$) are 35 and 3 km², respectively; $\underline{n}$ indicates within-patch population size. Dotted lines indicate a net value or population size ($\underline{P}_t$) for the sum of habitat patches over a region or forest.

<u>Pair</u>	<u>Number of young produced</u>
1	1
2	3
3	2
4	3
	—
	9 (five males, four females)

Density: The 33 individuals identified above reside in patch 1 (35 km^2). Patch 2 (3 km^2) is 3.0 km away and uninhabited. With size of patch 1 equal to 35 km^2 , density in patch 1 is 33 individuals/ 35 km^2 , or 0.94 individuals/ km^2 . Since this is well below carrying capacity ($1.2 \text{ individuals}/\text{km}^2$), no individuals leave patch 1.

Year Two

Population Age structure of the female population is now four 1 year-olds, four 2 year-olds, four 3 year-olds, and four 4 year-olds. Assuming each reproductive age female produces two young, 16 young are added to the population for a total of 49 individuals.

Density: Density in patch 1 is then 49 individuals/ 35 km^2 , or 1.4 individuals/ km^2 . Since this is over carrying capacity, emigration is expected. To reduce population size to $1.2 \text{ individuals}/\text{km}^2$, or 42 individuals in patch 1, seven animals emigrate to patch 2. Since patch 2 is fairly close, probability

of survival is close to one, and patch 2 will be filled to capacity (four individuals/ $3.0 \text{ km}^2 = 1.3/\text{km}^2$). However, three individuals would not survive, as both patches are full. Total population size over the forest would be 46 marten.

This example illustrates a highly simplified case, with only density-dependent mortality and simple survival curves. However, the decision theory and network analysis frameworks and their applicability to forest management are obvious. With a series of simulations, probabilities of sustaining a designated population size under different management alternatives (different patch sizes and inter-patch distances) can be determined.

Quantitative Life History

1. Demographic Parameters

Little is known about marten reproductive capabilities, the reproductive life span of females, or life expectancy. Marten mate in July-August, delaying implantation of the blastocyst until January-February (Ashbrook and Hanson 1930, Marshall 1951, Jonkel and Weckwerth 1963). Parturition occurs approximately 27 days after blastocyst implantation (Jonkel and Weckwerth 1963), taking place in February-June, most often in April (Marshall 1951, Ingles 1965, Maser et al. 1981). Females do not breed until two years of age and do not produce their first young until age three, because of delayed implantation (Soutiere 1978).

Some litter size records are available. Seton (1909) reported that marten litter sizes range from one to five and average three to four. Ingles (1965) also reported litters of up to five young, while Maser et al. (1981) reported litters of one to six, usually two to four. Markley and Bassett (1942) documented litter sizes of captive marten ranging from one to four, with 2.6 reported as an average. Wynne (1981) found two females, each with a litter of two. O'Neil (1980) also documented a female with a litter of two. A reasonable estimate of average litter size of marten appears to be two or three. However, litter size is probably dependent on factors such as population density, female nutrition, and reproductive history during the preceeding years. Ingram (1973) stated that females in poor condition have smaller litters.

Estimates of juvenile survivorship are not available. However, observations by Grinnell et al. (1937:200) led them to suggest, ". . . the number of young which reach maturity each year is remarkably

small." Jonkel (1959) presented evidence of high mortality or emigration for juvenile females: only three of 27 marked juvenile females were recaptured the following breeding season. In addition, of 66 marked juveniles, almost 11% were captured by commercial trappers before one year of age.

The normal and maximum life span of marten in the wild is not known. Markley and Bassett (1942) reported data from captive marten, stating that an animal could be expected to live and reproduce for at least 10 years and documented a litter of young produced by a 9-year-old female. Weckwerth (1957) estimated minimum ages of marten in a population in Glacier National Park, Montana. His data (Table 1) indicate that some animals reached an age of at least 5.5 years. Brown (1980), by counting cementum annuli in a premolar tooth, ascertained the age structure of a marten population in New York. Although verification of this technique is needed using known-age marten, these data probably represent the most accurate age-structure data available. The sample size is small; however, Brown's data (Table 2) show that only two of the 11 females are of reproductive age. In addition, males appear to have a greater life expectancy than females.

Table 1. Sex ratio and minimum age structure of marten populations in Glacier National Park (from Weckwerth 1957).

Sex	Minimum age (years)				
	1.5	2.5	3.5	4.5	5.5
Males	0	1	2	3	3
Females	1	1	1	1	1

Table 2. Age and sex structure of a marten population in New York (from Brown 1980).

Age	Males		Females	
	<u>n</u>	<u>%</u>	<u>n</u>	<u>%</u>
Juvenile	6	20.7	6	54.5
1	8	27.6	2	18.2
2	4	13.8	1	9.1
3	5	17.2		
4	3	10.3	2	18.2
5	1	3.4		
6	1	3.4		
7	1	3.4		
	<u>29</u>	<u>99.8</u>	<u>11</u>	<u>100.0</u>

Assuming the average life span of female marten is 4 years, two reproductive seasons would be available, or each female would have the potential to produce two litters. Assuming an average of 2.5 young/litter, five young could be produced by an average female in her life time. If the sex ratio of young at birth was 50:50, a female could produce 2.5 females. Thus, 40% of the juvenile females would need to survive to reproductive age (3 years) to replace the breeding female cohorts in a population. These cursory estimates illustrate the importance of obtaining data on reproduction, number and size of litters, and survivorship to three years of age.

Another determinant of population viability is sex ratio. Marten sex ratios are often skewed towards a higher proportion of males (Table 3). Given populations of the same size, those with a preponderance of males would have a lower reproductive capacity than a population with a 50:50 sex ratio. One reason for the disparate sex ratio may be

Table 3. Marten population sex ratios as calculated from the literature

Source	Sex ratio (males:females)
Grinnell et al. (1937)	3:1
Marshall (1951)	1:1
Newby and Hawley (1954)	1:1
Miller et al. (1955)	2:1
Hawley and Newby (1957)	2:1
Weckwerth (1957)	2:1
Jonkel (1959)	1:1
Soutiere (1978)	2:1
Major (1979)	1:1
Brown (1980)	3:1

that males are more easily trapped because of their larger home range or perhaps decreased trap wariness compared with females. A second explanation may be a real difference in the actual sex ratio due to higher female mortality or increased female sensitivity to environmental conditions. When the literature values are compared (Table 3), males outnumbered females in seven of the ten (70%) studies. Assuming that the disparate sex ratios are a reflection of true population sex structure, sex ratios are variable, perhaps because of environmental conditions. Management strategies may affect marten sex ratios, since sex-specific differences in habitat use have been noted (Soutiere 1978, Steventon 1979, Steventon and Major 1982). However, factors responsible for the deviation from an equal adult sex ratio remain to be identified.

2. Seasonal Marten Movements and Habitat Use

Marten use a variety of coniferous and, to a lesser extent, deciduous forest types and exhibit some seasonal and sex-specific

variability in use patterns. The key to understanding marten abundance and distribution lies in the ability to quantify habitat use and identify variability in terms of life requisite availability. The first step towards this goal, then, is to identify patterns of habitat use by monitoring marten movements and activity patterns.

Since winter and early spring are probably the most critical periods for marten due to high energy demands and reduced prey availability, identification and quantification of habitat use during that time is essential. Steventon (1979) studied winter habitat affinities of marten in northern Maine and compared marten use of clear-cut forests with partially cut mixed woods and uncut softwoods. Clear-cut areas were used less than expected, based on availability, while the other two forest types were heavily used. Over winter, females were found only in large blocks of residual forest and rarely crossed clear-cuts. Simon (1980) also noted that heavily logged areas were avoided in winter but were used in summer if slash or canopy cover were present. Hargis (1981) found that marten in winter in Yosemite National Park used all forest stand densities in proportion to availability. However, the marten exhibited a zig-zag pattern of travel, choosing similar microhabitats within the variety of forest stand densities. Preferred microhabitats had complete overhead cover less than 3 m above the snow. Campbell (1979) found winter hunting confined to dense stands of mature coniferous forest with hunting activity primarily below the snow (sub-nivean). Burgason (1977) related snow depth to canopy cover, reporting lowest snow depths in two uncut softwood stands, compared with three different age classes of clear-cuts. In addition, Koehler et al. (1975) found that stands with less than 30% overhead cover received the most

use when snow depths were less than 0.3 m (12 in). Marten in Ontario in winter occurred in coniferous stands and mixed woods with a high percentage of conifers, while mixed woods dominated by hardwoods and hardwood stands received little use (Francis and Stephenson 1972). These authors also found an inverse relationship between the proportion of coniferous cover and snow depth in a forest stand. However, they hypothesized that factors other than snow depth, such as shelter from wind and availability of logs and stumps, made coniferous areas more favorable to marten. Raine (1983) presented a contrasting opinion, based on studies of fisher (Martes pennanti) and marten in southeastern Manitoba. Although fisher activity was affected more by snow cover than by marten activity, both species traveled on hare and their own trails more frequently in midwinter (when snow was soft and thick) than in early (light snow cover) or late (crusty snow) winter. He hypothesized that this pattern is a means of energy conservation, as compacted snow trails provide relative ease of movement. Soutiere (1978) also noted a change in marten activity with a change in snow cover. He reported that marten traveled in clear-cuts when there was little snow, but not in late winter when snow depths increased. The effect of vegetation structure on snow depths thus may be a factor governing winter marten distribution.

Simon (1980) suggested that large logs are especially important in winter, for shelter and as prey access sites. Marten rely primarily on subnivean shelters in winter. Of 31 winter resting sites examined by Steventon and Major (1982), all except one were subnivean. Nineteen of the subnivean shelters were in natural cavities around decaying stumps,

two were under standing snags, seven were under hummocks of unknown origin, and three were under hummocks formed by bulldozed debris.

In summary, three habitat elements appear of primary importance to marten: overhead cover, fallen trees and stumps, and vegetation to support microtine and sciurid prey. In winter, coniferous overhead cover may decrease snow depths and thus decrease the energetic costs of travel. Fallen trees, stumps, and slash provide access to relatively uncommon small mammal prey in winter.

Seasonal Diet, Prey Distribution, Foraging Energetics

1. Seasonal Diet

To predict marten distribution and abundance patterns, an understanding of seasonal diet is required, along with knowledge concerning the degree of flexibility in switching prey bases.

Small mammals compose the major portion of the marten diet through most of its range. Cowan and Mackay (1950) reported that small mammals composed 76% of the summer diet and 91% of the winter diet of marten in Alberta. A similar pattern (i.e., the predominance of mammals in the diet) also has been reported in Colorado (Remington 1951), Alaska (Lensink et al. 1955), British Columbia (Quick 1955), Wyoming (Murie 1961, Campbell 1979), Montana (Weckwerth and Hawley 1962), Ontario (Francis and Stephenson 1972), Idaho (Koehler et al. 1975), Northwest Territories (More 1978, Douglass et al. 1983), Maine (Soutiere 1978, 1979), and California (Hargis 1981, Zielinski 1981).

Marten avoid or rarely prey on the ubiquitous and often abundant deer mouse (Peromyscus maniculatus) (Remington 1951, Weckwerth 1957, Weckwerth and Hawley 1962, Soutiere 1978). The preferred prey are microtines, primarily the red-backed vole. Four probable reasons (Zielinski 1981) for the preference of voles versus deer mice are the reported high densities of voles in specific vegetation types, the greater body weight of voles (a vole body weight is usually $\geq 50\%$ that of deer mice), vole use of runways and thus more predictable escape routes, and the winter torpor exhibited by deer mice, which may make their detectability more difficult for predators.

Various items compose the remainder of the marten diet. Other prey found in the diet by Cowan and Mackay (1950) included birds (summer,

5.9%; winter, 1%); insects (summer, 7.9%; winter, 0%); and berries (summer, 5.9%; winter, 3.8%). Campbell (1979) found mammals in 88% of 145 scats, vegetation in 23.4%, birds in 8.3%, and insects in 4.8%. Seton's (1953:494) description of the marten diet included, ". . . partridge, rabbits, squirrels, chipmunks, shrew and mice; birds, birds' eggs, fledglings, frogs, toads, fish, insects, and mice; . . ." and reptiles, nuts, berries, honey, and carrion. Zielinski (1981) documented remains of a weasel (Mustela sp.), yellow-bellied marmot (Marmota flaviventris), and a porcupine (Erethizon dorsatum) each in one or two scats. Quick (1953a) also documented porcupine as prey in marten stomachs. Pikas (Ochotona princeps) may serve as an occasional meal, as Lutton (1975) observed them giving alarm calls when marten approached. In captivity, marten feed on an extraordinary array of items, including small mammals, rabbits, birds, wheat cereal, berries, raisins, candy, insects, spaghetti, bread, celery, and lettuce (Remington 1952).

The marten diet is most diverse from late spring through early fall and least diverse in midwinter (Zielinski 1981). The winter diet also consists of larger prey items. For example, the winter diet included a high (20-40%) percentage of snowshoe hare in Ontario (Clem 1977), chickaree (Tamiasciurus douglasii) (21.9%) and snowshoe hare (14.4%) in California (Zielinski 1981), and red squirrel (T. hudsonicus), snowshoe hare, and northern flying squirrel (Glaucomys sabrinus) in Montana (Marshall 1946). Quick (1955) found evidence that a higher diversity of prey items was taken during the colder of two winters. He hypothesized that this was because of the inaccessibility of small mammal prey during the colder winter. Thus, marten had to forage over a larger area and encountered a greater diversity of food items.

2. Prey Distribution

Although marten appear to be opportunistic hunters, taking advantage of a variety of food items when available, they are limited primarily to mammalian prey in winter. In fact, Soutiere (1978) hypothesized that winter habitat use (use of dense forest) was governed more by prey availability and accessibility than by amount of overhead cover per se. Efforts to determine prey distribution should concentrate on prey species important in the winter diet and the effect of forest management on that prey distribution. It is assumed that winter, when small mammals are the primary prey, is the critical period.

The single most important species reported in the marten diet is the red-backed vole. Tevis (1956) studied small mammal response to logging of Douglas-fir (Pseudotsuga menzeisii) in northwestern California, examining 11 cutovers that ranged in age from 3 months to 20 years. Red-backed voles were found almost exclusively in uncut coniferous forest. The few specimens captured in cuttings were associated with logs, leading him to suggest that elimination of such logs caused extirpation of voles. In westcentral Oregon, Gashwiler (1959, 1970) found that red-backed voles were relatively unaffected by logging, as did Soutiere in Maine (1978). However, a postlogging burn eliminated the species from the Oregon study area. Before logging, the vole population was larger on the area to be cut than on the control. Following logging and burning and throughout the 10-year study red-backed voles were not captured on the area. Burgason (1977) examined three clear-cuts from 20 to 25 years of age, 14 to 16 years of age, and 6 to 10 years of age but obtained inconclusive results regarding the effect of logging on red-backed voles. Specifically, the control area

in year one of the study had a higher number of voles than all three clear-cut areas, while the following year the pattern was reversed.

What factors govern the distribution of red-backed voles?

Gunderson (1959) suggested that local distribution of voles in Minnesota was governed by free water availability. Other authors, working in Idaho (Koehler et al. 1975, Koehler and Hornocker 1977) and Wyoming (Campbell 1979), have noted the affinity of voles for mesic sites.

Voies also exhibit a preference for downed logs (Tevis 1956, Gunderson 1959), which may influence their distribution. Clear-cut and burned areas without fallen trees evidently do not provide adequate vole habitat, nor do extremely dense timber stands that prevent growth of lush herbaceous vegetation needed by voles (Koehler et al. 1975).

Campbell (1979) found selective cuts retained their mesic conditions and small mammal species composition remained approximately the same, while the clear-cuts became xeric and were dominated by deer mice. Snowshoe hares decrease initially in clear-cut areas, but begin to reoccupy these sites in approximately six to seven years. Their numbers peaked roughly 20-25 years following timber harvest in Maine (Burgason 1977). Red squirrels make little use of young clear-cuts, preferring uncut softwood stands (Burgason 1977).

Retention of mesic conditions sufficient for herbaceous ground cover development and of fallen trees, and thus red-backed voles, may be a key to maintaining marten habitat. Quantitative data are needed on the microhabitat requirements of important prey species such as the red-backed vole, snowshoe hare, and red squirrel.

3. Foraging Energetics

The long, cylindrical body shape and short fur of mustelids appear to be adaptations for a predatory existence at the expense of energetic efficiency. Worthen and Kilgore (1981) measured the metabolic rate of marten relative to a variety of air temperatures, finding a metabolic rate in thermoneutrality 12% higher than predicted by the standard mammalian equation (Kleiber 1961). This was primarily due to high thermal conductance (poor insulation) of their fur along with high surface to volume ratios. Brown and Lasiewski (1972) found the increased surface area and decreased insulation of long-tailed weasels (Mustela frenata) increased metabolism of cold-stressed animals 50-100% over that of a normally shaped mammal (Neotoma spp.). Moors (1977) determined the resting metabolic rate of an average male weasel would be approximately 34% higher than predicted. Farrell and Wood (1968) reported the basal rate of female mink (Mustela vison) averaged 12% more than predicted by their body mass. In addition, Casey et al. (1979) found oxygen consumption of the least weasel (M. rixosa) greater than predicted by body mass. Iversen (1972) studied the basal metabolic rate of seven mustelid species, reporting that for animals ≥ 1 kg, metabolism was roughly 20% higher than predicted by the standard mammalian equation, and even higher in the smaller (< 1 kg) species, up to 100% in the weasels.

In addition, activity patterns often appear energetically maladaptive. Zielinski et al. (1983) reported that marten were nocturnal in winter when temperatures were lowest, and diurnal in summer when temperatures were highest. Energy conservation would dictate a differing strategy of winter diurnality and maximal activity during

hours when temperatures are warmest. Zielinski et al. (1983:395) felt the observed pattern, "...optimized foraging time by expressing a flexibility of activity that permits adaptation to prey activity regimes after the prey exceed an availability threshold."

Winter, then, may place marten in an energy deficit situation. To optimize foraging benefits they are active when thermoregulation costs are high, they must gain access to subnivean prey, and the cost of travel through snow is probably high. A predictive model (Ackerman et al. in press) may be suitable for estimating the energy required for costly activities such as movement and maintenance of a steady state, along with the number of prey required by marten. This information may also provide a means of estimating habitat suitability for marten.

The model uses a summation of basal energy requirements, energy requirements for three activity classes, and added costs of growth and reproduction to predict age and sex specific energy requirements. In addition, we have added a parameter to account for increased costs associated with thermoregulation. Total energy required (E_{TOT}) is composed of basal metabolism (E_{BMR}), activity costs (E_{ACT}), growth costs (E_{GRO}), reproductive costs (E_{REP}) and thermoregulatory costs (E_{TH} , applied only when the animal is in ambient air temperatures below thermoneutrality). Since not all ingested energy is assimilated and available to the organism, energy lost in urine and feces is added to the energy requirements to yield total required energy intake.

Energetics models often use the Kleiber (1961) equation for estimating basal metabolic rate using body mass:

$$\underline{M} = 70 \underline{W}^{0.75} \text{ where } \underline{M} = \text{basal metabolic rate (kcal/day)}$$

$$\text{and } \underline{W} = \text{body weight (kg).}$$

However, mustelids in general have a greater metabolic rate than predicted by their body mass (Farrell and Wood 1968, Iversen 1972, Casey and Casey 1979, Casey et al. 1979, Worthen and Kilgore 1981). To date, marten metabolic rate has been studied only by Worthen and Kilgore (1981), and their data indicates $\underline{E}_{\text{BMR}}$ is 12% higher than predicted. Thus, their value of 81.27 kcal/day is used in this model. This gives a mass specific metabolic rate of 78.3 kcal/kg/day (using their reported average weight of 1.038 kg).

Activity data were placed into three classes, Class I being the least active and Class III the most active. Class I includes sleeping, lying down, lying down with head up, looking around, "comfort movements," grooming, standing, and feeding quietly. Class II activity was walking, vigorous feeding, and other active but localized behavior. Trotting, running, prey capture, dragging a kill to a cache site, playing, and courtship were Class III behaviors. Activity costs ($\underline{E}_{\text{ACT}}$) were expressed as a multiplier of basal metabolism where:

$$\underline{E}_{\text{ACT}} = \underline{AC} \times \underline{E}_{\text{BMR}} \text{ in kcal/day}$$

$$\text{where } \underline{AC} = (\underline{a}_i \times \underline{p}_i),$$

$$\underline{a}_i = \text{energetic cost of activity in class } i,$$

$$\underline{a}_1 = 0.3 \text{ (i.e., 30\% above } \underline{E}_{\text{BMR}})$$

$$\underline{a}_2 = 3.5$$

$$\underline{a}_3 = 9.0$$

and,

$$\underline{p}_i = \text{proportion of time in activity class } i.$$

Chappell (1980) determined that energy costs of arctic mammals on the snow surface were 15-25% greater than the costs of living in

subnivean space (under snow), even when the sun was shining. On a clear night these costs were 40-50% greater than remaining beneath the snow. Given the data collected by Zielinski (1981) and Zielinski et al. (1983), marten may spend a considerable amount of energy for thermoregulatory costs during their nocturnal winter foraging bouts. To apply a thermoregulation cost, lower critical temperature (T_c) at which the animal can maintain body temperature without additional energy expenditure must be known. Worthen and Kilgore (1981) estimated T_c to be 29 C. This lies within the range of values (25 to 30 C) reported by Casey and Casey (1979) for weasels (*M. rixosa* and *M. erminea*). However, it is considerably above the range (-20 to -30 C) reported by Powell (1979) for active fishers.

For this model, we used a conservative estimate of a 30% increase in metabolic costs during marten activity periods when ambient temperatures are below the critical level. In addition, a T_c (lower critical temperature) of 30 C was used. The equation for additional thermoregulatory costs is then:

$$\underline{E_{TH}} = 0.3 \times \underline{E_{BMR}} \text{ when } \underline{T_a} \text{ (ambient temperature) is less than 30 C.}$$

Both gestation and rearing costs were included in female reproductive costs. Breeding occurs in June or July through August, however due to delayed implantation births do not occur until February to April. Time between implantation and parturition is approximately 27 days (Jonkel 1959, Jonkel and Weckwerth 1963), with a lactation period of 2 to 2.5 months (Deblaay 1980). The cost of pregnancy was equal to the cost of fetal growth to 28 g at birth (Brassard and Bernard 1939), plus 27% (7.6g) for associated fluid and tissue production. Cub energy

requirements (E_{CUB}) after birth were calculated in the same manner as adult requirements:

$$E_{\text{CUB}} = E_{\text{BMR}} + E_{\text{ACT}} + E_{\text{GRO}} \text{ in kcal/day,}$$

$$E_{\text{REP}} = n_{\text{lit}} \times E_{\text{CUB}} \times e \text{ in kcal/day,}$$

where n_{lit} = number of cubs in a litter and

e = energy transfer efficiency (60% during lactation and 100% during gestation and after weaning).

To estimate the number of prey required, seasonal diets of marten must be known, along with energy content of the prey item and the fraction of energy remaining after digestion and assimilation. Although no estimates of marten digestive efficiency are available in the literature, trials have been done using fisher. Davison et al. (1978) determined the portion of energy remaining after fisher digestion and assimilation was 76.7% on a diet of snowshoe hare and 73.9% on a small mammal diet. The values developed for fisher (Davison et al. 1978) are similar to those for mink (Roberts and Kirk 1964), badgers (Taxidea taxus) (Jense 1968), and least weasel (Golley 1960). Pending development of this type of data for marten, the use of values obtained for fisher probably represent a minimal source of error.

To obtain energy available per prey item, data on energy per gram body weight of prey items are needed. Davison et al. (1978) determined the gross energy contained in several mammalian species including the snowshoe hare (4.69 kcal/g), and meadow vole (Microtus pennsylvanicus) (5.16 kcal/g). Mean body weights of the red-backed voles were 15.4 g for males and 15.1 g for females in Colorado in October (Merritt and Merritt 1978) with significantly higher and lower weights in spring and

winter, respectively. Burt (1957) reported that snowshoe hare weights ranged from 1.4 to 1.8 kg (3-4 lb). Using these data, the average red-backed vole (15.25g) would contain 78.69 kcal, assuming kcal/g are roughly equivalent to that for the meadow vole. The average snowshoe hare (1.6 kg) would contain 7,504 kcal.

The applicability and usefulness of this model to marten management can be illustrated using a hypothetical marten population of four, assigning values to required parameters, and estimating the number of voles and snowshoe hares required to sustain the population over winter (September through February). For simplicity, we assumed no growth or reproduction occurred over this period. The proportion of time in each activity class was: Class I, 50%; Class II, 40%; and Class III, 10%. In addition, increased thermoregulation costs were applied to time in activity classes II and III (i.e., 50% of total hours in a day). For the four marten:

$$\underline{E}_{\text{BMR}} = 4(81.27 \text{ kcal/day}) = 325.08 \text{ kcal/day},$$

$$\begin{aligned} \underline{E}_{\text{ACT}} &= 4([(0.5 \times 0.3) + (0.4 \times 3.5) + (9 \times 0.1)] 81.27) \\ &= 796.44 \text{ kcal/day}, \end{aligned}$$

$$\underline{E}_{\text{TH}} = 4(0.5 [0.3 \times 81.27]) = 48.76 \text{ kcal/day}, \text{ and}$$

$$\underline{E}_{\text{REP}} \text{ and } \underline{E}_{\text{GRO}} = 0.$$

For a diet consisting of 100% voles:

$$\text{vole biomass consumed per day} = \frac{(325.08 + 796.44 + 48.76)}{5.16 \text{ kcal/g} \times 0.739} = \frac{306.9 \text{ g}}{\text{voles/day}}$$

where 5.16 kcal/g = energy value of voles

and 0.739 = percentage of energy remaining after digestion and assimilation.

$$\begin{aligned}\text{Number of voles required over winter} &= \frac{3.06.9 \text{ g voles}}{\text{day}} \times \frac{\text{vole}}{15.25\text{g}} \times 181 \text{ days} \\ &= 3,642.5 \text{ voles.}\end{aligned}$$

For a diet consisting of 50% voles and 50% snowshoe hares:

$$\text{vole biomass consumed per day} = \frac{(325.08 + 796.44 + 48.76) 0.5}{5.16 \text{ kcal/g} \times 0.739} = 153.44 \text{ g voles/day}$$

$$\text{Number of voles required} = \frac{153.44 \text{ g}}{\text{day}} \times \frac{\text{vole}}{15.25\text{g}} \times 181 \text{ days} = 1,821.1 \text{ voles.}$$

$$\text{Hare biomass consumed per day} = \frac{(325.08 + 796.44 + 48.76) 0.5}{4.69 \text{ kcal/g} \times 0.767} = 162.66\text{g hare/day,}$$

where 4.69 kcal/g = energy value of snowshoe hares

and 0.767 = percentage of energy remaining after digestion and assimilation.

$$\text{Number of hare required} = \frac{162.66\text{g hare}}{\text{day}} \times \frac{\text{hare}}{1600\text{g}} \times 181 \text{ days} = 18.4 \text{ hares.}$$

Thus, the required winter prey is 1,821 and 18 capturable voles and hares, respectively. Given the assigned parameter values, habitat containing less than 1,821 capturable voles and 18 capturable snowshoe hares or less than 3,642 capturable voles would not sustain a marten population of four over winter. These calculations will be easily applied to realistic marten populations when field data are obtained.

Given data on prey distribution patterns and the effects of management strategies on these patterns, the suitability of different forest tracts for marten may be determined.

SUMMARY

1. The current range of the marten is a small portion of the historic range. Extensive habitat destruction and fragmentation along with trapping and fire are the major factors which have impacted the marten range.
2. The reported declines in marten numbers are attributed to their low biotic potential and affinity for habitats that have been reduced. These factors in combination with their large home range size and natural curiosity make marten vulnerable to trapping.
3. Information needed to effectively manage marten in the central Rocky Mountains includes a description of marten reproductive biology, population dynamics, habitat use, and movement patterns.
4. Seven integrated studies are recommended to provide knowledge of factors governing marten distribution and abundance for predicting and evaluating effects of various forest management practices on marten populations. They include:
 - A. Network flow analysis and decision theory: an integrated, quantitative model to plan forest management for marten population goals.
 - B. Demographic parameters of marten populations in the central Rocky Mountains.
 - C. Seasonal movements and habitat use by marten.
 - D. The marten HSI model: a quantitative evaluation.
 - E. Occurrence and diversity of prey species in the marten diet with emphasis on winter diet.

- F. Abundance, distribution, and habitat use of prey species in the marten diet.
- G. Population dynamics and bioenergetics of the marten.

5. In summary, forest and wildlife managers need methodologies whereby forest management strategies can be evaluated in terms of the probability of marten extinction associated with each strategy. Based on the literature reviewed for this problem analysis, three approaches seem appropriate. The habitat suitability model may provide the most cost effective, short-term evaluation of marten habitat. However, the approach lacks the quantitative demographic aspects necessary to assess local and/or regional marten populations. The energy flow approach will provide a quantitative, site-specific approach to ensure that most resources are available to maintain a marten population. Most important, decision theory and network analysis will provide a means to simulate local and regional marten population dynamics in a mosaic of habitat patches varying in size and distribution over time. Thus, land use strategies that minimize the risk of marten extinction yet allow for multiple forest use can be chosen. The latter approach offers the forest manager and biologist the greatest latitude in decision making, yet retains a quantitative framework easily integrated into dynamic programming methodology for use in timber management. The recommendation is to proceed with all three approaches, but place long-term and major emphasis on a model that incorporates network flow theory and decision theory.

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